



# Savi's Pipistrelle *Hypsugo savii* (Bonaparte, 1837)

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## Common Names

English	Savi's pipistrelle
German	Alpenfledermaus
French	Vespère de Savi
Spanish	Murciélago montañero
Italian	Pipistrello di Savi
Russian	Кожановидный нетопырь

## Taxonomy and Systematics

The prior name of the species is *Vespertilio savii* Bonaparte 1837 (type locality: Pisa, Italy); however, in most of the older literature it is reported under the name *Vesperugo maurus* Blasius, 1853 suggesting its relations with species now comprised within the genera *Pipistrellus* and *Nyctalus*. With regards to differences from these bats, Kolenati 1856 placed the species in the separate genus *Hypsugo*. Most subsequent authors classified the species within the genus *Pipistrellus*, often as a separate group within that genus (Miller 1907, 1912; Tate 1942; Ellerman and Morrison-Scott 1966; Hill and Harrison 1987; Koopman 1994), yet the doubts on its generic assignment persisted. Due to its resemblance to *Eptesicus* in dental and external characters, the species was either included in that genus (in subgenus *Amblyotus*, e.g., by Ognev 1928) or considered as an element of support for the identification of a large genus *Vespertilio* covering all clades of *Pipistrellus-Vespertilio-Eptesicus* grade proposed, e.g., by Kuzyakin (1950). Much later,

Horáček and Hanák (1985) and Menu (1987), who analyzed the taxonomic distribution of characters used in vespertilionid taxonomy (dentition, baculum, penial morphology, postcranial skeleton, karyology, etc.) for a large set of taxa belonging to *Vespertilio* sensu Kuzyakin (1950), demonstrated a distinct position of *savii* and several forms closely related to it (*darwini*, *alashanicus*, *velox*, *corrensis*, *ariel*, *arabicus*, *austrianus*, *pulveratus*, *mordax*, *affinis*) and suggested to place the species in a separate genus, *Hypsugo* Kolenati, 1856. Distinct differences from *Pipistrellus* were also supported by further morphological comparisons (Hill and Harrison 1987 who proposed *Hypsugo* as a subgenus of *Pipistrellus*) and by electrophoretic data (Ruedi and Arlettaz 1991).

Volleth (1989), Volleth and Heller (1994) found that *Hypsugo* shared chromosomal apomorphies with Vespertilioninae rather than Pipistrellinae. Arguments for a separate generic status of *Hypsugo* were discussed in details by Horáček et al. (2000). The generic status of *Hypsugo* was finally supported by the study of mtDNA (Hoofer and Van Den Bussche 2003), which generated approximately 2.6 kilobase pairs of mitochondrial DNA (mtDNA) sequence encompassing three adjacent genes (12S rRNA, tRNAVal, 16S rRNA) for 120 vespertilionids representing 110 species, 37 of 44 genera, and all subfamilies. At the same time, the study confirmed that the genus *Hypsugo* is a polytypic clade. Recent assessment (Simmons 2005; Burgin 2019) recognized 18 species within the genus, distributed mostly in the Oriental and Ethiopian

regions. Recently, Hutterer et al. (2019) segregated sub-Saharan taxa into a separate genus *Parahypsugo*.

In the traditional view, within its W-Palaearctic range, several forms of this species have been considered as subspecies (Simmons 2005): they were described as *Vespertilio ochromixtus* Cabrera, 1904 (type locality: Sierra de Guadarrama, Spain), *Scotophilus darwini* Tomes, 1959 (Las Palmas, Canary Isl.), *Vesperugo caucasicus* Satunin, 1901 (Tiflis = Tbilisi, the Caucasus), and *Amblyotus tauricus* Ognev 1927 (Karadagh, Crimea). The latter two were downgraded to a subspecies rank (Bobrinskii et al. 1944) and are now considered clear synonyms of *H. savii* without assignment to any distinct subspecies (Pavlinov and Lissovsky 2012). However, the situation with the remaining forms and taxonomic status of the traditional *H. savii* is more complicated, in particular with regards to recent molecular studies.

Pestano et al. (2003) demonstrated a deep divergence between individuals of *H. savii* from mainland Spain and the Canary Islands (6.3–7.2% in uncorrected cytb and 3.8–4.4% in 16S rRNA), contrasting to shallow divergences among individuals from different islands of the Canary archipelago. Mayer et al. (2007) reported considerable difference between a bat caught in Morocco and *H. savii* from European mainland (9.6% in nd1). Regarding similar sequence differences observed by Pestano et al. (2003) between individuals from the Iberian Peninsula and the Canary Islands, Mayer et al. (2007) suggested a separate species status for putative clade colonizing the NW Africa, Spain, and Canary Islands provisionally denoted as *Hypsugo* cf. *darwini* (Tomes, 1859). Veith et al. (2011) found the haplotypes close to this clade also in Sicily and Sardinia, and Dondini et al. (2016) reported it from a small island of Montecristo near coast of Tuscany, Italy.

Another molecular study by Ibanez et al. (2006) analysed mitochondrial (Cytb and ND1) and nuclear (RAG2) DNA sequences for each of the 28 bat species known for Iberia, and found three different lineages in the European samples of *H. savii*. One lineage was represented by two bats from southern Iberia, whereas another lineage was found as far north as Switzerland. These

two lineages are sympatric in Andalusia, southern Spain. The third lineage corresponds to Savi's pipistrelles from the Eastern Mediterranean. Recently, the Iberian lineage was found on Malta (Mifsud and Vella 2019). The third lineage in the sense of Ibanez et al. (2006) was later discovered in Turkey (as Clade 2 in Çoraman et al. 2013). The divergences between the clades were relatively high; Clade 2 (South-eastern Europe and Near East) differed from Clade 1 (South-western Europe) by ca. 7% on ND1 and 8% on Cytb and by ca. 9% on ND1 and 8% on Cytb from Clade 3 of Çoraman et al. 2013 (North Africa and Iberia). Mayer et al. (2007) reported a mitochondrial DNA sequence from one Israeli sample of *H. cf. savii* (nd1) that differed by 13.8% from other sequences of the species from the same area.

In short, the respective data suggest appearance of at least four distinct clades of *H. savii* within the W Palaearctic: (1) Southern Levant, separated by the deepest divergence from the others, supposedly extending in the southern part of the range, (2) E-Mediterranean clade recorded in Croatia, Turkey and Levant (including Israel), (3) W-Mediterranean lineage (for which the name *H. ochromixtus* Cabrera, 1904 is available) recorded from Spain to Switzerland, (4) SW Mediterranean (including NW Africa and S Spain) clade supposedly close to Canarian *H. darwini*, recently recorded in Sardinia, Sicily and Tuscany. The emerging view, supported by multiple records of sympatric distribution of particular clades (1 and 2 in Israel, 2 and 3 in Spain, 2 and 4 in Sardinia and Italy), suggests separate species status for all these clades. Unfortunately, until present day such a conclusion would be quite premature for several reasons.

First, the available samples are quite insufficient in both size and geographical coverage. In most instances the published studies have examined just a few individuals relying only on a single mitochondrial marker, often using a different one (cytb, nd1, 16SRNA). A complex investigation providing relevant data on patterns in genetic variation within particular populations and their geographic correlates, cross-controlled by application of multiple markers, both mitochondrial and nuclear, is missing. The relationships between

particular clades and type populations, based on the names available for nomenclature expression of phylogenetic divergences (within West Palearctic in total 12 names – Simmons 2005), were not examined in details, and except for *H. darwini* (in Canary Islands), they are not obvious. Prior to answering these question by profound comparative studies (including elucidation of actual distributional status of particular clades), any taxonomical proposal is to be regarded as a provisional hypothesis only.

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## Paleontology

Similar to other non-cave-dwelling species, *H. savii* appears only exceptionally in the fossil record. A single mandible assigned to the species was found in cave deposits of the Early Middle Pleistocene age in Hundsheim, Austria (Rabeder 1972). The species was further reported in interglacial assemblage of the Mikulino(= Eemian) age in Matuska Cave, Russian Caucasus (Rossina et al. 2006), a Late Pleistocene site Aquilón P7 in Spain (Galán et al. 2016), and in Holocene sites in Italy (Riparo Salasini, Salari and Kotsakis 2011) and southern Hungary (Mélyvölgyi-kőfülke cave, formerly identified as *Eptesicus nilssonii* – Görföl et al. 2010). The Early Preboreal record from Býčí Skála cave (Czech Republic) demonstrates the species' range expansion in the Early Holocene almost at the modern northern range margin in Central Europe and its capacity for considerable range dynamics (Horáček et al. 2014).

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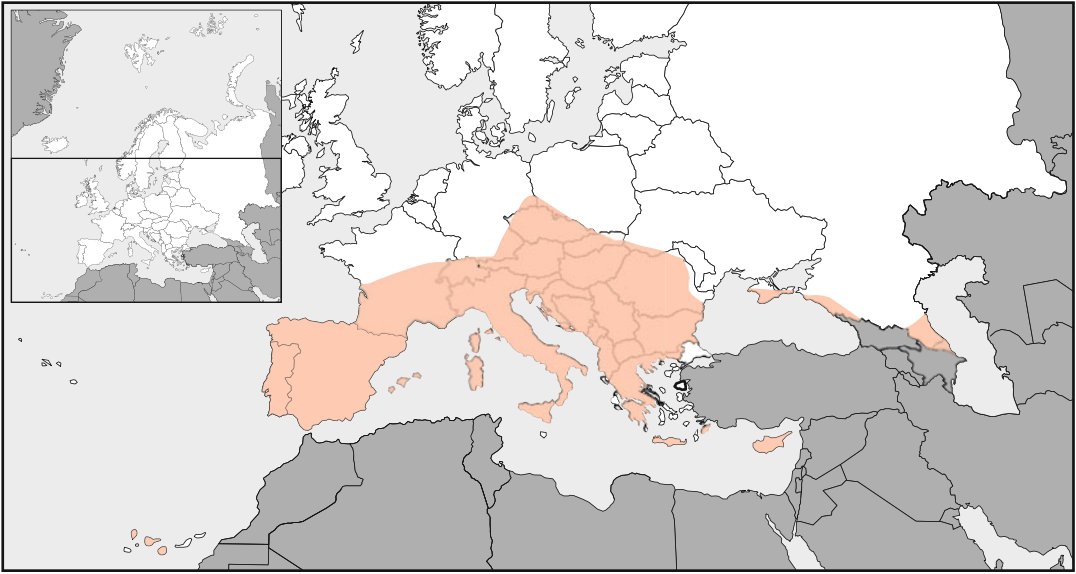
## Current Distribution

The Savi's pipistrelle is a thermophilous species that occupies a large W Palearctic range from W Mediterranean to Central Asia, Afghanistan, and Middle East, allopatric to E Asian ranges of its sister clades. The center of its European range is the Mediterranean region. *H. savii* is a typical inhabitant of rocky habitats. Most records come from mountain regions, yet it occurs at a wide range of altitudes from coastal areas up to 3,300 m above sea level

(Garrido-Garcia 2000). The species' current range in Europe spans across the Mediterranean region (including many islands) from Spain, France, and Italy to the Levant region (Israel, Lebanon, W Syria, Hatay province in Turkey) of the Eastern Mediterranean and the Balkans (all countries of the region) and Carpathians to West Ukraine (Juste and Paunović 2016). The temporal shift of the northern range margin of the species was reviewed by Reiter et al. (2010) and Uhrin et al. (2015), indicating a continuing range expansion after 1990. Until 1990 the northernmost range margins passed along the Danube in Bulgaria and Serbia, and only a single historical record was reported from the north of the Alps (Horáček and Benda 2004). Currently, the species regularly occurs in most regions of Slovakia and the Czech Republic including records of breeding colonies (Reiter et al. 2010; Jahelková et al. 2014) up to the Děčín district (northern Bohemia, Czech Republic) near the German border (Bartonička et al. 2017). Occasional vagrants or transported animals have been documented in Britain (Fisher 1998) and in Hamburg and Wuppertal in Germany (Ohlendorf et al. 2000; Skiba 2010). Recently, a male was found in Dresden and a breeding population was ultimately reported from Leipzig (Ohlendorf 2019) (Fig. 1).

However, earlier findings (Lehmann and Engemann 2007) imply that a resident population might colonized Saxony even before.

It is uncertain whether some Romanian and all Ukrainian records that derive from acoustic data reflect real presence of the species or represent misclassified calls of other bats (e.g., *Pipistrellus kuhlii*). Yet, any evidence of netted bats or otherwise documented specimens are still lacking for the Ukrainian Carpathians (L. Godlevska, pers. comm.). New records of the species come predominantly from urban areas, and the species' spread is often associated with its synanthropic roosting behavior (Uhrin et al. 2015), and convenient microclimatic roost conditions (Reiter et al. 2010). At the same time, climate change may also contribute to the range expansion in Europe (Rebelo et al. 2010; Ancillotto et al. 2018). On the other hand, no range expansion has been observed both in Southern Ukraine and in the south of Russia (Gazaryan, unpublished data).



Map template: © Getty Images/iStockphoto

**Fig. 1** Distribution is based on the IUCN Red List of Threatened Species. Version 2017-2, Article 1F reports and author's own data. (Map template: © Getty Images/iStockphoto)

*Hypsugo savii* is one of the most common and widespread bats in the Levant region with numerous records in W Syria and Lebanon (Benda et al. 2006, 2016) reaching the southern range margin in northern Israel (Mendelssohn and Yom-Tov 1999). Although it does not rank among common species in Turkey, and most of its Turkish records come from the coast areas, *H. savii* is most probably distributed throughout the entire Anatolia (Benda and Horáček 1998; Karataş and Sözen 2006).

In the Transcaucasia, *H. savii* was recorded across Georgia (Bukhnikashvili et al. 2004), Armenia, and Azerbaijan (Rakhmatulina 1999, 2005). In the North Caucasus, the species was recorded only from Krasnodar Region and Dagestan (Gazaryan and Dзамirzoyev 2005; Gazaryan 2007). From the Caucasus, the range stretches further eastwards through Iran to Central Asia and northern Afghanistan, with Hindu Kush mountains as a natural border of the species range (Benda and Gaisler 2015). In Iran, *H. savii* is particularly common in the northern regions but

its records are scattered also in most other mountain regions of the country including the eastern Baluchistan where the species reaches the southernmost margin of its range (Benda et al. 2012). The bats from Mongolia formerly considered as *H. savii* (comp. Horáček and Hanák 1985) in fact belong to *H. alaschanicus*, a species ranging from Mongolia to Japan (Horáček et al. 2000). This outlook is supported by current molecular studies (Datzmann et al. 2012). The record from the North Africa are restricted to the mountain regions of N Atlas and the Mediterranean coast regions in Morocco, Algeria, and Tunisia, while the species is absent from Libya and Egypt (Juste and Paunović 2016). The molecular data (16S RNA) suggest a close relationship between the North African population and individuals from Sardinia and Sicily, and the populations of the Canary islands (Tenerife, El Hierro, La Gomera and Gran Canaria) tentatively referred to a separate taxon of unconfirmed species status, *H. darwinii* (Pestano et al. 2003, also see section on “Taxonomy and Systematics”).

## Description

### Size and Morphology

*Hypsugo savii* (Fig. 2) is a small-sized bat species in comparison to other Palearctic bat species (length of forearm 30–37.3 mm, weight 4.5–9.0 g, hind foot <8.0 mm). The ears are short (length 11.5–16.0 mm) and broadly rounded, the basis of the earlobe ascends from below the eyes (Horáček and Benda 2004). The tragus is blunt and at its broadest width almost as wide as the length of its inside margin (length of tragus 4.7–7.0 mm), the antitragus is not so evident but still marks a delineation in the conch. Its wing membranes, muzzle, and ears are very dark to black. The wings are moderately broad and pointed. The plagiopatagium attaches at the base of the toe. The Post-calcarial lobe (epiblema) of the tail membrane never contains a transversal cartilage slat (as in genus *Pipistrellus*) and can vary from a narrow edge along calcar up to a considerable overlap. The tip of the tail projects outside of the tail membrane by one or two last vertebrae (3.0–5.0 mm). The penis is characteristic in its morphology and is bent under a right angle between its root and apex, enlarging distally with a baculum that is placed within the distal half of the penis. Baculum is long like in pipistrelloid bats but flat, roof-like on section (not rounded as in pipistrelloid genera), with



**Fig. 2** Savi's pipistrelle from Croatia (photo by Marina Kipson)

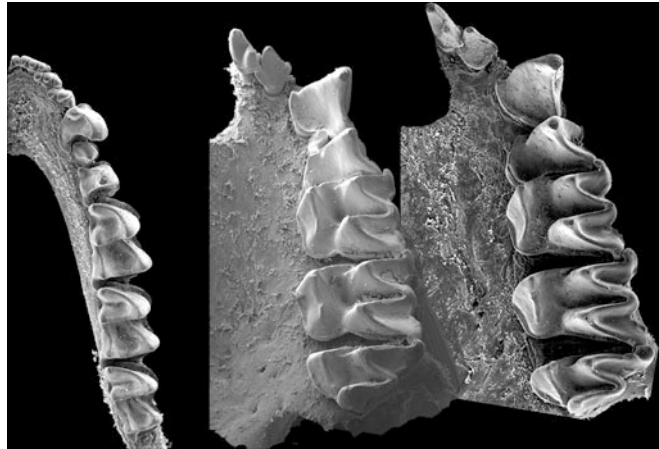
disc-like terminal enlargements above the urethra muzzle, unique among Palearctic vespertilionid bats. The skull is more robust than in other *Pipistrellus* species, the rostrum is relatively broader, shorter and more compact having its dorsal surface flattened thus making the dorsal profile of the frontal region more straight or convex (condylobasal length 12.0–14.5 mm). The ridges on the edge of orbits are very pronounced (similar to *Vespertilio*) and the zygomatic arch lacks dorsal broadening. The postmaxillary part of the palate is longer than in *Pipistrellus*, and the mandibula is short. The coronoid process is blunter than in *Eptesicus* or *Vespertilio* and not directed forwards unlike in such genera, whereas the processus angularis is thicker and longer than in *Pipistrellus*. The basisphenoid pits are absent (Horáček and Hanák 1985; Horáček and Benda 2004).

The humerus shows characteristics similar to those of *Eptesicus* and *Pipistrellus* species of the same size, yet its proximal epiphysis is somewhat narrower and certain differences are observed in shape of its distal epiphysis: a broad processus spinosus does not extend to the level of the distal margin of trochlea and the epitrochlea basin is less pronounced. The vertebral column consists of 38 vertebrae, the caudal part of sacrum is not shortened, the first tail vertebra is narrower than tail margin of the sacrum, and the tibia is roughly of the same length as the femur (whereas it is clearly longer than the femur in *Pipistrellus*).

### Dentition

Dentition is myotodont and more robust than in *Pipistrellus* spp. The dental formula is  $i\ 2/3, c\ 1/1, p\ 1-2/2, m\ 3/3$ , total 32 or 34. *Hypsugo savii* has a broad and bicuspid I1, while I2 is unicuspid, well developed and reaches the height of the second cusp of I1. The upper canine is wide with a distinct crest terminating at inflated distal margin of the crown which appear in direct contact with P4. P2 is small, displaced to the inner side of the tooth-row parallel to distal margin of canine or (in ca 20% of individuals) it is missing entirely (comp. Figure 3). The large upper premolar P4 is broad

**Fig. 3** Occlusal view of the lower and upper dentitions (with and without P2) of *Hypsugo savii* (specimens from Bulgaria)



and short and lacks the cingular cusps and distinct talon basin. The first and second upper molars are robust with high protocones and post-protocrista terminating with well pronounced hypocones. The protoconal fossa is broad with a spacious distal slope: paralophs, metalophs as well as trans- or distocristas are entirely missing. M3 is moderately reduced with completely retained metacone. The lower incisors are trifold, all of roughly the same size overlapping each other by about half of a tooth width. The c1 is broad with a distinct posterior basin, only slightly higher than the molar protoconid. The lower premolar p2 is small, rounded on section of a half-height of p4 that is square on section with slightly enlarged cingular basin at lingual distal crown margin. The lower molars are large, showing  $m1 > m2 > m3$  scaling. The talonids are much wider than trigonids. In m1 and m2, all molars are distinctly myotodont with a high-staying poscristid and large distally tapered hypoconulids at the lingual base of the crowns. The talonid of m3 is completely retained and relatively long.

### Pelage

Compared to the true pipistrelle bats, adult *H. savii* are characterized by a conspicuously contrasting coloration pattern: almost black membranes, muzzle, and auricles; bright white pelage

at ventral side; and warm brown coloration on the back with gold hair tips. At the same time, the species exhibits an extraordinary variability in dorsal fur coloration. Dulic (1975) recognized six different types of dorsal hair coloration from specimens found on the Dalmatian islands, with the most frequent one described as having lighter ochraceous hair tips and dark brown base with completely dark head. Similarly, in southern France and Switzerland, the majority of animals has bicolor dorsal fur (81% and 76.1%, respectively) (Arlettaz et al. 1993). Dorsal hairs of bicolored individuals are dark brown to blackish at base with golden, beige, or blond coloration at apical tips; exceptionally, hairs can be even grey with silver tips. However, although this is the most typical phenotype of *H. savii*, some individuals can be unicolor. On Dalmatian islands, this color type was found in 2.8% of the individuals, possibly associated with young animals. In southern France and Switzerland, this type occurs in 19 and 24% of bats respectively, being present regardless on the age structure of individuals (Arlettaz et al. 1993). Individuals from the Levant region and Middle East are exclusively bicolored, the pale apical part takes more than one third of dorsal hair length by which their dorsal coloration tends to be of a paler appearance (Benda et al. 2006, 2012). Ventral pelage is bicolor, hairs are relatively long with dark bases and bright white tips.

## Age Determination

As a general rule, the coloration of juvenile *H. savii* is less contrasting in comparison to adult individuals – the membranes, face, and muzzle are greyish brown, and the pelage lacks a distinct bicolor pattern. The pelage of juveniles is dark greyish brown on the dorsal side and without bright whitish pattern on the ventral side. However, the reliability of these characters is questioned by the broad variation observed in this species (see above). In juvenile or yearling male bats, the disc-like distal termination of baculum is not completely ossified.

## Physiology

Studies on the thermal physiology of *H. savii* showed that the species can undergo longer periods of overheating on a daily basis, making it potentially more resistant to extreme heatwaves (Kuzyakin 1950; Ancillotto et al. 2018). The peak body temperature measured within the study in Italy reached 46.5 °C (Ancillotto et al. 2018). This is the highest body temperature ever measured in a free-ranging bat. Both males and females performed daily overheating bouts and torpor bouts at least once during the study period (average of three consecutive days and nights per individual), although there were significant differences in temperature oscillations between males and females. In females, oscillations of body temperature were narrower with both torpor and overheating bouts lasting less and being shallower or less intense than in males (Ancillotto et al. 2018).

## Genetics

### Cytogenetics

The karyotype (in G-banding aspect) retains the ancestral arrangement known for the Vespertilionid bats that also appears in genera such as *Myotis* or *Pipistrellus*: the diploid number of chromosomes (2n) is 44, and the

fundamental number (FN) is 55 (Volleth 1989; Zima et al. 1991; Reina et al. 1995). From autosomal chromosomes, three pairs are large and one pair is medium metacentric, the rest of the 17 pairs are acrocentric and vary in size from small to large. The X chromosome is a medium-size metacentric one, whereas the Y chromosome is dot-like acrocentric (Reina et al. 1995). Volleth (1989) and Volleth and Heller (1994) demonstrated that *H. savii* exhibits an apomorphic arrangement of the autosome 11, the character shared with other clades of Vespertilionini. The nucleolus organizer region (NOR) is situated in chromosome 15 which also possesses a secondary constriction below the centromere (Volleth 1989; Reina et al. 1995).

### Phylogeography

Based on mitochondrial markers (cytb and nd1), two haplotypes can be found in the Iberian Peninsula, one of which restricted only to the southern tip of the peninsula, whereas a third haplotype is distributed in the eastern Mediterranean (Ibanez et al. 2006). This distinction, however, was not that clear by using a nuclear marker RAG2, leaving the relationships among lineages unresolved probably due to a slower mutation rate of the nuclear marker (Ibanez et al. 2006). On the other hand, the divergence between mainland Spain and the Canary Islands was 6.3–7.2% in uncorrected cytb and 3.8–4.4% in 16S rRNA, suggesting a monophyletic origin of both lineages, whereas the divergence among individuals on the Canary Islands themselves was much lower (Pestano et al. 2003). Another study based on mtDNA (nd1) and 16S rRNA showed that a specimen from Morocco differed from the European lineage by 9.6%, showing at the same time a close relationship with those from the Canary Islands (Mayer et al. 2007). Based on 16S rRNA, Veith et al. (2011) demonstrated that two haplotypes of *H. savii* occur on Sardinia, one belonging to the European *H. savii* lineage and another one forming a group with specimens from Sicily, the Canary Islands, and Morocco (Pestano et al. 2003; Mayer et al. 2007). A particularly deep divergence



(13.8%) is suggested by a single individual from Israel (Mayer et al. 2007).

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## Life History

No systematic data on the annual life cycle and life history traits are available. The available anecdotic observations concerning reproduction can be summarized as follows. Birth dates span from the beginning of June to the end of July. In Croatia, pregnant females were found from mid-June until the end of July (Dulic 1970) and the appearance of subadults peaked from the end of July until mid-August (Dulic 1958, 1970). In Bulgaria and northern Greece, the majority of births are thought to occur from the beginning until mid-June (Dietz et al. 2009), although a pregnant female was also caught in Greece in the second half of June (Hanák et al. 2001). However, findings of subadult animals in the Eastern Rhodopes in Bulgaria in the middle and at the end of July confirm that births mainly occur in the first half of June (Ivanova and Gueorguieva 2004; Tilova et al. 2005). In the Middle East, lactating females were caught in the beginning of June ( $n = 6$ ) (Benda et al. 2006). Pregnant females from Syria ( $n = 2$ ) had two embryos (Benda et al. 2006); two out of three pregnant females from Bulgaria carried two embryos (Horáček and Benda 2004), and bats in captivity ( $n = 6$ ) had two pups attached to their nipples (Vergari and Dondini 1998), suggesting that twins are common in this species. Spermatogenesis probably occurs in May, and in the first half of June testes are still abdominal whereas in the first half of July they descend to the scrotum and subsequently enlarge to reach their summer maximum (Horáček and Benda 2004).

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## Habitat and Diet

### Spatial Movements

There are only two radio-tracking studies up to date that followed spatial movements of the species, one from Italy and the second one set in

Croatia. In Italy, home ranges of males and females measured on average  $2.0 \pm 1.3 \text{ km}^2$ , with the mean straight distance between roosts and foraging areas being  $2.9 \pm 1.6 \text{ km}$ . In the study, home range size in males was almost twice as that of females, and males also travelled longer distances than females (Ancillotto et al. 2018). In Croatia, a radiotracking study on reproductive females found that the median home range size of pregnant females was  $50.8 \text{ km}^2$ , whereas the median of lactating females was  $24.1 \text{ km}^2$ ; however, home range sizes (95% kernel) were not significantly different between the two conditions. The maximum straight distance from the roost to the foraging site was  $14.2 \text{ km}$  in pregnant females and  $9.3 \text{ km}$  in lactating females (Kipson et al. 2018). In the latter study, pregnant females could regularly cross a sea channel near the roost to reach the mountain slopes on the other shore (the shortest distance for crossing the sea channel was  $3.3 \text{ km}$ ), whereas lactating females did not cross the sea and in general stayed closer to their roosts (Kipson et al. 2018).

## Habitat Selection

*Hypsugo savii* is primarily a lithophilous species that inhabits Mediterranean habitats rich in cliffs with sub-xeric bushy vegetation. It also occurs in a broad spectrum of other habitats from coastal wetlands to sub-mountain grasslands or woodland areas in mountain valleys. The altitudinal range of its records spans from the sea-level to the alpine zone, including the current European altitudinal record for a bat of  $3300 \text{ m a.s.l.}$  (Garrido-Garcia 2000). Most of the records come from the sub-mountainous and mountainous regions (Ibanez et al. 1992; Juste and Paunović 2016). However, the recently expanding populations also colonized the medium altitude and lowland regions (Paunović et al. 2015).

Foraging habitats are influenced by a considerable individual variation and a quite versatile pattern of habitat selection. In Croatia, pregnant females preferred rocky pastures, followed by forest, meadows and riparian vegetation, and showed lower affinity to illuminated areas

(villages), shrubland and sea. Lactating females showed a greater tendency to forage in riparian habitats. These habitats were followed in importance by meadows, forest and rocky pastures (Kipson et al. 2018). The difference in habitat preferences between reproductive stages of females may reflect prey availability, e.g., swarming insects, within each time period rather than expressing a tight connection to a certain habitat type. Similarly, the preference for forests was primarily related to hunting above the canopy and above clear cuts in open space (Kipson et al. 2018). In Italy, males and females primarily preferred extensive farmland, followed by mixed-coniferous woodland, broadleaved woodland, urban-discontinuous, scrubland, and rocky areas. Within individual home ranges, extensive farmland was still the most preferred habitat type followed by scrubland (Ancillotto et al. 2018). Although some observations and acoustic studies in urban areas indicated that Savi's pipistrelle actively forages at street lights (Vernier 1995; Paunović et al. 2015), neither radio-tracking study (Ancillotto et al. 2018; Kipson et al. 2018) confirmed the supposed preference for foraging in urbanized areas. In fact, the species is not prone to hunt at artificial lights in the presence of more suitable habitat types with sufficient availability of insects. Older studies on *H. savii* habitat preferences were primarily based on observational or acoustic surveys, on which bases the species appeared to hunt above tree crowns (Gaisler 1994), around cliffs and rocks (Dulic 1970), above mountain meadows, freshwater sources (Di Salvo et al. 2009; Russo and Jones 2003), ant colonies (Dietz et al. 2009), over the sea surface (Dulic 1970), and around and above street lamps in urbanized areas (Vernier 1995). The species was also observed hunting during daylight hours (Dulic 1970).

## Diet

Diet records based on fecal pellet analyses show a considerable between-region variation supposedly due to local and seasonal differences in

food availability and to the opportunistic feeding habits of the species. Unfortunately, a large-scale study analyzing seasonal changes in diet composition is still missing.

The diet analysis presented by Beck (1995) for Switzerland indicated Lepidoptera and Diptera as the most frequent prey (in 53% and 48% of fecal pellets), followed by Hymenoptera (in 30%), Neuroptera (in 30%) and Hemiptera (in 18%), whereas Coleoptera and Trichoptera were found only in 2% and 3% of fecal pellets, respectively. In pellets from south Kyrgyzstan and Bulgaria predominant prey was given by small Cicadoidea (10–60%), Heteroptera (10–40%), and small Lepidoptera (10–30%), with other groups represented in smaller quantity (Aphidoidea 10–20%, small Coleoptera 5–10%, Diptera 5–10%, Hymenoptera 5–10%, Neuroptera 5%) (Horáček and Benda 2004). Further records of *H. savii* diet from the Mediterranean and the Middle East confirm the species' strategy of taking advantage of high concentrations of swarming insects: in Syria, the main prey were Formicoidea, Heteroptera, Coleoptera, and Lepidoptera (Benda et al. 2006), Coleoptera and Formicoidea were the main diet components in Turkey (Whitaker and Karataş 2009), and Hymenoptera (mostly Formicoidea), Coleoptera, and Heteroptera prevailed in the diet in Lebanon and the Greek islands (Žďárská 2013). Similarly, in Dalmatia (Croatia) faecal pellets contained almost exclusively Formicidae (Dietz et al. 2009). In a detailed diet comparison between pregnant and lactating females in Croatia, ants were a staple in the species' diet in both study groups, with lactating females consuming larger quantities of this prey, followed by Heteroptera in both groups; Aphioidea, nematoceran Diptera and Coleoptera were consumed more often by pregnant females. Other prey items consumed by both groups of females did not differ between reproductive periods (namely, Heteroptera, Lepidoptera, Culicidae, Auchenorrhyncha, Neuroptera, Hymenoptera, and Brachycera). Prey items that were only marginal and occurred in pregnant females included Dermaptera, Orthoptera, Blattodea, Psyllinea, whereas Trichoptera occurred only during the lactating period (Kipson et al. 2018).

## Behavior

### Roosting Behavior

In natural habitats, *Hypsugo savii* is a lithophilous species, primarily roosting in rock fissures situated in cliffs and other rocky habitats, usually occupied by solitary individuals or small groups. Therefore, these natural roosts are very difficult to find and describe. In urbanized environments, however, the species exhibits a pronounced tendency to colonize fissure roosts in buildings. In northern parts of the range, a preference for artificial structures represents a prevailing characteristic of its roosting strategy (Uhrin et al. 2015). The majority of data on the roosting biology of *H. savii* report the species to use a variety of human-made structures rather than rock crevices, but this may be due to the fact that the latter are more difficult to observe. Specifically, roosts were found in attics (Freitag 1996), behind roof gutter and roller type shutters (Vernier 1995), various cracks and voids in historical buildings and ruins (Benda et al. 2006), in a fissure on a balcony (Stoycheva et al. 2009), in abandoned shepherd cabins (Strelkov and Shaimardanov 1983), and in fissures in tunnels (Stojanovski 1994). Similarly, most records from the newly colonized area of Central Europe, i.e., Hungary, Austria, Slovakia and Czech Republic, come from urban environments (Uhrin et al. 2015), however older records from buildings are also known from the Mediterranean (Dulic 1958; Vernier 1995). The species is in fact common in buildings in countries such as Italy (D. Russo, pers. comm.). Roosting in rocky fissures was reported many times throughout the species range, e.g., in Kyrgyzstan (Rybin et al. 1987), Transcaucasia (Rakhmatulina 1995), West Syria and Lebanon (Benda et al. 2006, 2016) or Balkans (Benda et al. 2003), and southern Spain (Garrido-Garcia 2000), yet this was established mostly based on visual records of individuals or small colonies leaving their fissure roosts. Besides roosting in shallow crevices in rocks, a new type of roost for a European bat species was noted for the first time in individuals of *H. savii* that were using ground-level space below a rock as their daily shelter (Alcalde and

Gosá 2009). Frequent roosting in ground-level rock vertical crevices was also confirmed in a study from Croatia, where the highest number ( $n = 43$ ) of *H. savii* roosts in natural habitat were discovered (Kipson et al. 2014).

The number of individuals within a colony is usually  $<20$  (Stojanovski 1994; Dietz et al. 2009; Ancillotto et al. 2018), and the most numerous colonies in Croatia contained between 20–40 bats (Dulic 1958), and 30 bats in Bulgaria (Stoycheva et al. 2009). Mean colony size in Italy was  $1.8 \pm 1.0$  for males and  $5.6 \pm 1.7$  for females, respectively (Ancillotto et al. 2018). In Croatia, pregnant females mainly roosted solitarily in ground-level rock crevices, and formed small groups shortly before parturition (2–5 individuals), whereas lactating females were found in groups of 2–9 individuals (Kipson et al. 2014). In Italy and Slovakia, mixed colonies with *Pipistrellus kuhlii* were reported (Danko 2007; Ancillotto et al. 2018). There are almost no reports of hibernacula of *H. savii*; few records of hibernating bats refer to single individuals found in crevices near cave entrances (Paunović et al. 2015, Benda et al. 2016). It is thought that the species hibernate in small groups inside rock fissures and cracks as well as in buildings (Rakhmatulina 2005; Quetglas and Garrido 2005), whereas single individuals were found to hibernate in fissures in building walls in Austria (Spitzenberger 1997), Italy (GIRC 2004) and Bulgaria (Stoycheva et al. 2009).

### Group Behavior and Social Structure

Lactating females switch their roosts, probably following a fission-fusion model in which members of one social group (classified as occupying the same roost at the same time) showed repeated splitting and merging of subunits belonging to the group. This type of behavior was observed in Croatia, where lactating females and their young switched roosts and either split or merged with other females on different nights, indicating that they belonged to the same social group whose cohesion is flexible over different nights (Kipson et al. 2014). However, this type of behavior was so

far noted on a small sample and only in one region so it warrants a more detailed investigation before generalizing to all populations.

Regular associations in a common night roost were observed in several sites in Bulgaria, Lebanon and Crete (Horáček unpublished data). This behavior took place in spacious rocky overhangs, high cave entrances or in large human constructions like abandoned factory halls, empty warehouses or a village assembly hall. Individual bats used to appear there about 1 h after sunset with maximum abundance (up to ca 10–20 individuals) around midnight. Arriving bats used to combine temporal swarming flights with resting at separate roosting places without forming pairs or clusters. In a few sites the behavior was observed over several successive nights and for several years. Regular congregations in common night roosts may allow social integration, whereas daytime roosts used only temporarily by single individuals have as such reduced social significance.

## Foraging Behavior

The species is an aerial hawk, and hunts its prey in open space, often utilizing locally abundant aerial swarming insects (see section “Diet”). In general, *H. savii* depends on the abundance of prey at various habitat types rather than on any particular habitat type (Kipson et al. 2018). Recent radio-tracking studies revealed preference for more natural habitats when available. Therefore, it is rather an urban-tolerant species than an urban exploiter (Ancillotto et al. 2018).

## Echolocation

The echolocation signals of *H. savii* have a typical FM/QCF structure, characterized by two distinct elements: a sharp frequency modulation (FM) component continued with shallower frequency modulation, reaching an almost constant frequency – quasi-constant frequency or QCF (Russo and Jones 2003). The species can be distinguished from bats in the *Pipistrellus* genus because its signals have lower end frequencies

and frequencies of maximum energy, whereas the same values are higher than those in genus *Eptesicus*. In the Swiss Alps, call parameters were measured as followed: start frequency at 32.4 kHz, central frequency 32.8 kHz, end frequency 32.0 kHz, sweep bandwidth 2.2 kHz, interpulse interval comprised between two values, 192 and 294 ms (Zingg 1988). A second study from Switzerland showed that the mean call duration was 7.3 ms, lowest call frequency 28.8 kHz, frequency of peak energy 34.9 kHz and highest frequency 48.3 kHz (Obrist et al. 2004). In Greece, the parameters had slightly higher mean values, starting frequency was at 55.5 kHz, ending frequency at 33.7 kHz, frequency of peak energy at 36.7 kHz, bandwidth 8.7 kHz, duration of the signal 6.8 ms and the inter-pulse interval was 148.5 ms (Papadatou et al. 2008). In Italy, mean values were as followed: start frequency 47.3 kHz, end frequency 32.8 kHz, frequency of maximum energy 34.6 kHz, middle frequency 35.1 kHz, duration 8.1 ms and inter-pulse interval 170.7 ms (Russo and Jones 2002). Although echolocation call parameters of *H. savii* can overlap in range with those of *Pipistrellus kuhlii* (a species with partially sympatric distribution) when the former calls in cluttered space, especially in open space the two species may be told apart with good confidence.

## Social Calls

Social calls of the species are known only from a single study (Nardone et al. 2017) and appear to show high flexibility and structure. Calls were either produced as a single unit or they were combined into a variety of associations containing 2–9 syllables. Social calls were assessed visually based on the shape of their spectrogram and were classified into five categories: “A - steep downward frequency sweep (FM) followed by a quasi-constant frequency (QCF) part, B - steep downward frequency sweep (FM) followed by a rapidly ascending frequency-modulated final part, C - Steep downward frequency sweep (FM) followed by a frequency modulated, highly variable final part, D - Narrow downward frequency sweep

(FM) followed by a frequency modulated part with a rapidly ascending frequency-modulated final portion, E - Steep downward frequency sweep (FM)” (Nardone et al. 2017). The trill like call (type E) was only used in multiple calls and was recorded only during mating season, indicating that it might be connected to reproduction. Single component social calls (types A to D) seem to be used quite often during flight in *H. savii*, whereas in other pipistrelle species they are emitted only occasionally. The calls showed in general complex combination of syllables as well as flexibility and rarely recurring motifs, indicating they might serve a wide range of scopes for the species (Nardone et al. 2017).

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## Parasites and Diseases

Endoparasites reported by Lanza (1999) included three species of Neobacteria, eight species of flatworms (Digenea), and one roundworm (Nematoda) species (Lanza 1999). In Serbia, 4 species of gastrointestinal digeneans were found in *H. savii*, namely, *Plagiorchis* sp., *Lecithodendrium linstowi*, *Prosthodendrium chilostomum*, *Mesotretes peregrinus* (Horvat et al. 2017). Ectoparasites in Lanza (1999) also included 21 species of mites and ticks (Acari), 5 species of bat flies (Nycteribiidae) and 9 species of flea (Siphonaptera). *H. savii* is a type host of a parasite belonging to Acari, *Spinturnix nobleti*, which was found and described for the first time for this bat species (Denuff et al. 1990).

A novel poxvirus detected for the first time in a bat in Europe (from an individual of *H. savii* in Northern Italy) was consequently named *Hypsugopoxvirus* (Lelli et al. 2019). The genome analyses of the poxvirus showed that it belonged to the *Chordopoxvirinae* subfamily and had the highest nucleotide identity (85%) to *Eptesipoxvirus* (EPTV) found in *Eptesicus fuscus*, in USA. However, the viral ecology and disease associations of the *Hypsugopoxvirus* are not known and need further research (Lelli et al. 2019). Similarly, two beta coronaviruses, closely related to the Middle East respiratory syndrome coronavirus, were obtained from this bat species (Moreno et al. 2017), as well as a novel astrovirus

sequence (Dufkova et al. 2015). However, more detailed information on these viruses are so far lacking. Specific antibodies to the European Bat Lyssavirus Type 1 neutralizing were detected in blood samples from the species in Spain (López-Roig et al. 2014). A prevalence of adenoviruses in *Hypsugo savii* (3 out of 50 samples) was reported for Iberia (Rossetto et al. 2020).

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## Population Ecology

The knowledge of population dynamics and intra and inter species interactions is currently lacking. The overall population of the species is experiencing a northward range expansion, which might be connected to climate change (Ancillotto et al. 2018) and to the synanthropic nature of the species (Uhrin et al. 2015). Climate change modelling scenarios made for European bats predicted that *H. savii* will experience a significant range expansion of >220% until 2060 (Rebelo et al. 2010). Within the last two decades, the species has expanded to the area north of the Alps and it seems that the expansion farther north is still ongoing (see more in section “[Current Distribution](#)”). Due to the fact that the species seems to be able to tolerate extreme heat by performing longer overheating bouts (Ancillotto et al. 2018), this bat might persist within its southern range across the Mediterranean despite climate warming, although it is not known how the increased heatwaves and drought might influence reproductive success.

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## Conservation Status

At the global level, *H. savii* is protected by the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and the Agreement on the Conservation of Populations of European Bats (EUROBATS). In Europe, it is listed in Appendix II of Bern Convention and Appendix IV of the EU Directive on the Conservation of Habitats, Flora and Fauna (92/43/EEC). Therefore, *H. savii* is legally protected in most countries within its European range. The species is classified as of Least Concern in both global and

European IUCN Red Lists because no major threats are identified and the range is expanding.

Nevertheless, in connection to wind turbines it is regarded as a high-risk species, frequently contributing to casualty counts, especially in the Mediterranean part of its European range (Rodrigues et al. 2015). The most probable reasons for *H. savii*'s vulnerability to windfarms are its aerial hawk strategy and the tendency to fly in open space, as well as its occurrence in mountain regions where windfarms are often placed (Alcalde and Sáenz 2004). For example, in northern Spain, as much as 62.5% of fatalities under wind turbines were individuals of *H. savii*, with the greatest mortality being recorded from August to October (Alcalde and Sáenz 2004). Furthermore, the first evidence of bat mortality at windfarms in Italy confirmed mortality of *H. savii* (6 out of 7 carcasses found) (Ferri et al. 2011), also ascertained for Croatia (Zagmajster et al. 2007). In a review of known fatalities at wind turbines in Europe (Rodrigues et al. 2015), *H. savii* was represented by 209 cases (53 from Croatia, 44 from Spain, 43 from Portugal, 30 from France, 28 from Greece, 10 from Italy and 1 from Germany). A remarkable case of mortality at a wind turbine was recorded outside its distribution range known at the time of the record, in the German state of Saxony-Anhalt (Lehmann and Engemann 2007). It seems that wind turbines can have a large impact on local populations of the species. However, the possible impact of windfarms on the structure and density of the European population remains unknown due to the lack of research.

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## Management

There is currently no known management on the populations of the species. The future impact of climate change and increasing droughts within the Mediterranean range of the species, might require active water retention management that would also benefit local populations for which it represents an important habitat type (Kipson et al. 2018). Similarly, due to roosting in human made

objects throughout species range, a potential conflict with humans might arise. Therefore, it will be necessary to preserve these roosts where possible and increase education and awareness among policy makers and general public.

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## Future Challenges for Research and Management

The Savi's pipistrelle is currently ongoing a northward range expansion, and as such presents an interesting model species to study, especially in the light of the changing climatic conditions and adaptability to roosting in human-made structures. However, until recently the species has gained very little research attention and detailed information on its ecology is largely lacking. The challenge is to gain a better insight into its ecology, from the newly colonized regions as well as from the historic core area of its distribution (e.g., roosting, foraging and diet, home range size, and habitat selection). Although the species seems to be well adapted to high temperatures, it is still questionable how potential future changes in climate will affect its reproduction and survival in the Mediterranean region. In places where wind turbines are being planned, monitoring and subsequently proper management of their effect on the species will need to be carried out. Future studies should also focus on resolving the taxonomic questions and genetic relations among the potential various clades within the species' European range.

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